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CHROMOSOME NUMBER POLYMORPHISM IN AN AUSTRALIAN PONERINE ANT

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Southern Victorian populations of *Rhytidoponera metallica* have $n = 22$ to 17, with progressive replacement of two acrocentrics at a time by a metacentric to yield numbers lower than 22 (*nombre fondamentale* = 23). A further collection with $n = 12$ represents either a further reduction in this Robertsonian system or a sibling species. Related species have $n = 21$ (*victoriae*) and 23 (*tasmaniensis*).

Introduction

Although the order Hymenoptera contains at least as many species as the order Diptera, only three cases of apparent or proven chromosomal polymorphism have been reported in it (Waterhouse and Sanderson, 1958; Crozier, 1968a, 1969). The present paper describes a widespread and extensive polymorphism in chromosome number found in the ponerine ant *Rhytidoponera metallica* in the state of Victoria, Australia.

Materials and Methods

Following colcemid pretreatment (Crozier, 1969), aceto-orcein squash preparations were made of cerebral ganglia of prepupae and worker pupae, and of pupal testes. The male material was preferred because the small chromosomes found in the karyotypes of this species are more easily traced in haploid than in diploid cells. The number of cells counted per individual as shown in Table I. A majority of cells in each case had the number shown for that individual, other counts being due to cell fragmentation. Suitable preparations were obtained from 18 individuals representing eight colonies and six localities.

Results and Discussion

Individuals from localities 1 to 5 (Fig. 1, Table I) have haploid numbers from 22 to 17; diploid (female) karyotypes of 43, 42 and 41 were also found. These karyotypes are related in a simple Robertsonian manner: one larger metacentric replaces two smaller acrocentric chromosomes for each decrease in number. Thus, 17-chromosome karyotypes possess six large metacentric chromosomes, but 22-chromosome karyotypes have only one. Fig. 2(A-C) shows haploid karyotypes with 17 chromosomes (six large metacentrics), 19 chromosomes (four metacentrics) and 21 chromosomes (two metacentrics). The same relationship can be seen in diploid cells (Fig. 2D-F), where one with 41 chromosomes possesses five metacentrics, one with 42 has four, and one with 43 has three. The *nombre fondamentale* is thus 23, although the presence of subacrocentrics among the small chromosomes (see Fig. 2C) reduces the utility of the *n. f.* concept in this case. Although there is a preponderance of haploids near 21, the absence of 18's and the diploid numbers 44, 40, and below 40 is probably due to chance.

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TABLE I

Chromosome numbers in *Rhytidoponera metallica*, showing haploid or diploid numbers for 18 individuals from six localities (compare with Fig. 1). Two colonies were sampled from Portsea and Parkville, one elsewhere. Numbers in parentheses represent the cells counted in each individual

Locality	*n*						*2n*			
	17	18	19	20	21	22	24	41	42	43
1. Portsea					1 (15)			1 (56)	1 (80)	
1. Portsea					1 (51)					
2. Parkville										1 (19)
2. Parkville						1 (48)				
3. Camperdown					1 (36)					
4. Dunkeld	2 (110; 55)		1 (85)	2 (46; 56)						
5. Zumstein's					1 (18)					
6. Beulah							5 (50; 27; 40; 68; 31)			

Fig. 1. Map of Victoria, Australia, showing localities of colonies sampled of *Rhytidoponera metallica*. Compare with Table I.

At present, due to their small size, I cannot distinguish individual chromosomes in *metallica* karyotypes apart from the obvious separation of large metacentrics from small acrocentrics. Therefore I cannot trace the geographic distribution of each set of one metacentric and its complementary acrocentrics, although this may be possible in the future, using an air-drying technique (Crozier, 1968b). There is also little evidence for broad geographic trends in chromosome number, such as found in the North American beetles *Chilocorus* and *Pissodes* (Smith, 1962), although it may be significant that one colony from a southwestern locality (locality 4) has the haploid numbers 17, 17, 19, 20, and 20, while higher numbers predominate elsewhere (Fig. 1).

Five individuals from another locality (locality 6 in Fig. 1) have a diploid number of 24 (Fig. 2G). I regard this as the diploid rather than the haploid number because the material examined consisted of worker pupae as well as unsexed prepupae. Although the Robertsonian system found in the other localities could, if extended, lead to this number, I hesitate to ascribe this karyotype to the same sequence because it includes three pairs of small acrocentrics and some larger subacrocentrics, although classification of some of these is difficult. The corresponding karyotype from the southern Robertsonian system would have only one small acrocentric pair, with the rest metacentric. I have two hypotheses for the relationship of this karyotype to the others. Firstly, the population at locality 6 may represent a sibling species. Secondly, further changes, probably pericentric inversions, may occur in intermediate populations, converting metacentrics in the hypothetical 12-chromosome 'southern' karyotype into acrocentrics, leading to a system

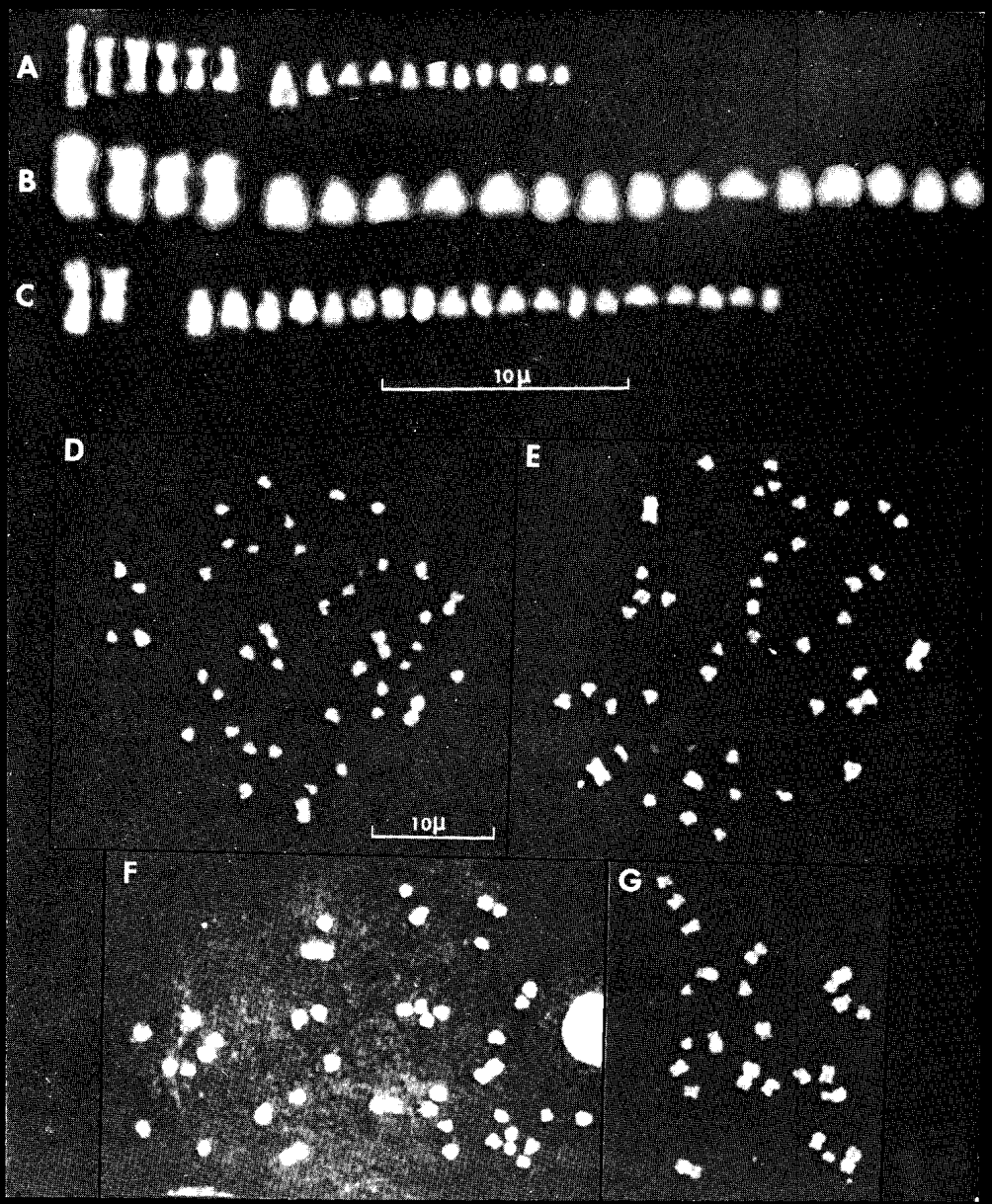

Fig. 2. Haploid (A, B, C) karyograms and diploid (D, E, F, G) karyotypes of *Rhytidoponera metallica*. (A) $n = 17$; (B) $n = 19$; (C) $n = 21$; (D) $2n = 41$; (E) $2n = 42$; (F) $2n = 43$; (G) $2n = 24$.

similar to that found in a 'hybrid swarm' of *Pissodes* species (Smith, 1962) where pericentric inversions and Robertsonian changes in one chromosome have yielded six different chromosomes combinable in 13 different ways.

R. metallica occurs widely in the southern two thirds of mainland Australia, except for the southwestern and southeastern corners of the country, where closely related species of *Rhytidoponera* are found (Brown and Wilson, 1956). In Victoria *R. metallica* is replaced in heavily forested country by *victoriae* and *tasmaniensis*. I found three individuals from one colony of *tasmaniensis* (one male, two female, taken at Dromana) to have haploid and diploid numbers of 23 and 46 respectively (Fig. 3A), while eight individuals of *victoriae* (three male, five female) from four colonies from three south-central Victorian localities (Narbethong, Cranbourne, Dromana) had 21 and 42. It is noteworthy that the *victoriae* karyotype (Fig. 3B) appears stable, numerically at least, and that it differs markedly from that of *metallica* in that the chromosomes do not vary so widely in size and in that they are nearly all acrocentric to subacrocentric (21-chromosome *metallica* karyotypes have two large metacentric chromosomes). These results suggest that most of the *metallica* karyotypes arose by centric fusions from a higher-numbered karyotype, rather than by 'fissions' from a lower-numbered one.

Of particular interest among other reports of chromosomal polymorphism in Hymenoptera is that of Waterhouse and Sanderson (1958), in which they describe chromosome number polymorphism in the sawfly *Tenthredo acerrima*. Most broods of this sawfly were found to have $n = 18$, $2n = 36$ except for one with $n = 21$, $2n = 42$. Upon crossing, these broods yielded offspring with variable numbers of chromosomes. Although these data are suggestive of a chromosome number polymorphism, the possibility cannot be excluded that sibling species are involved.

Samples from different localities of ants of the *Iridomyrmex "detectus"* group in Australia differ in the position of the centromere on two of the smallest

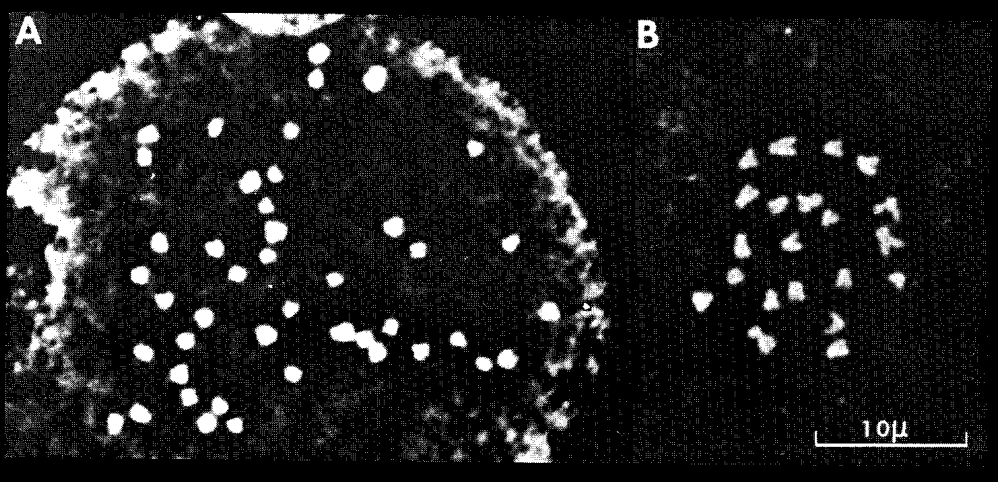

Fig. 3. Karyotypes of *Rhytidoponera tasmaniensis* and *R. victoriae*. (A) *R. tasmaniensis*, $2n = 46$. (B) *R. victoriae*, $n = 21$.

chromosomes (Crozier, 1968a). Of course, this also may not indicate actual polymorphism within a population, but rather interpopulation differentiation. The taxonomic status of the different populations is also in doubt.

Iridomyrmex gracilis, also of Australia, contains two 'chromosomal races', or sibling species (Crozier, 1969). One of these races appears to have an inversion polymorphism in one of the larger chromosomes of its karyotype, because one colony yielded diploid karyotypes with two large acrocentrics, but in those from another colony only one large acrocentric was seen, the place of the second being taken by a metacentric. Here, too, further data are needed, especially the discovery of the other homozygote.

Although Smith (1960) believes that chromosomal polymorphism could be quite prevalent in Hymenoptera, due to "the absence of chiasma formation in the haploid males," other authors (White, 1954; Suomalainen, 1962) have suggested that the possession of haploid males should very significantly reduce the genetic variability of hymenopteran populations compared with those of species with both sexes being diploid, due to the inevitable exposure of all loci to selection in a hemizygous condition. However, with appropriate viabilities for the various genotypes, heterotic polymorphisms can occur at sex-linked loci (Li, 1967a, 1967), and all hymenopteran loci can be considered sex-linked.

As pointed out by White (1954) and Kerr (see Rothenbuhler, Kulinčević and Kerr, 1968), sex-linked gene effects are likely to be of unusual importance in hymenopteran genetics (an example of sex-linked gene effects is furnished by the caste-determination loci of the bee *Melipona* (Kerr, 1950)). I have elsewhere (Crozier, 1969) summarized evidence of considerable genetic variability in some Hymenoptera, and I believe Kerr is probably correct in suggesting that hymenopteran species can have variability comparable to normal diploid species, and that this variability could be due to sex-limited gene effects at many loci. The actual extent of this variability, however, remains to be examined. Although Kerr (1967), by genetic load determinations, measured the strength of sex-limited effects in populations of the honey bee *Apis mellifera*, such inbreeding experiments cannot distinguish between few loci of large effect and many loci of small effect (Lewontin, 1967).

The occurrence of both 17- and 20-chromosome males in the same colony could be due to singular aspects of the biology of *metallica*. In this and related species, although winged females do occur, they are very rare, and most of the eggs in a colony are probably laid by a small percentage of inseminated workers (Brown, 1953; Haskins and Whelden, 1965). Males apparently fly from nest to nest, insemination taking place near or within each nest. Colonies of this ant should thus show more internal genetic variability than those of species with one laying female per colony.

The virtual absence of winged females also means that populations of this species may be 'genetically viscous' (Hamilton, 1964), with gene flow reduced to a degree dependent on male dispersal powers. One might therefore expect a greater degree of interpopulation differentiation than is reported here.

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